

Zonation of the Marine Fauna and Flora on a rocky shore near Singapore

By R. DENISON PURCHON, PH.D.

Raffles Professor of Zoology

and

I. ENOCH, B.SC.

University of Malaya, Singapore

(Received June, 1953)

Introduction

IT IS GENERALLY known that the fauna and flora of the inter-tidal zone are normally stratified, each species being largely confined to a particular vertical range. This applies not only to the fixed organisms such as the algae, corals, barnacles, etc., but also to those which are capable of considerable movement such as the gastropods.

As one passes upwards from low water mark of extreme spring tides (L.W.E.S.T.) to high water mark of extreme spring tides (H.W.E.S.T.), step by step the rigours of the environment become progressively more severe. The higher up the beach, the longer is the exposure to high temperatures, and to dessication by sun and wind. Each species is adapted to a particular mode of life, and is capable of surviving within a certain range of physical conditions. With regard to the fixed organisms, only those specimens survive whose larvae settled and attached themselves to the substratum within the appropriate zone in the littoral or sublittoral region.

The motile organisms, on the other hand, if dislodged from the most favourable level on the beach, by wave action for example, are capable of returning to the optimum level. They may indulge in considerable wanderings diurnally, yet they will not stray far from their optimum horizons, for their movements are regulated by the circumstances in which they find themselves. Certain species of gastropod, for example, tend to move upwards while they are submerged, but move downwards when exposed by the retreating tide. In this way they maintain the same vertical distribution on the beach from day to day.

The height of high tide varies rhythmically, rising at fortnightly intervals towards H.W.E.S.T., and falling at similar intervals towards high water of neap tides (H.W.N.T.). The stratification of the motile organisms in this part of the beach will be primarily related to the

height of high water, day by day, rather than to an absolute level above mean sea level (M.S.L.).

The conditions of life on a tropical beach are very different from those which obtain in a temperate climate. In the tropics the upper parts of the beach are subjected to very much more severe heating and dessication than is experienced in temperate regions, but are not exposed to the winter frosts of the latter. Moreover, the upper parts of the tropical beach are not protected from dessication, and extremes of temperature, by a thick algal canopy as may be the case on a temperate shore. For these reasons it was a matter of great interest to the writers to examine the zonation of the intertidal fauna and flora of a tropical rocky shore, to determine whether there are any major differences in the scheme of zonation from that which is typical of temperate regions.

The Stephenson (1949) indicated that the exhaustive study of zonation in one particular area may lead to an intricate system of zonation which, though fitting the local facts, may by its very detail obscure the broader principles of zonation, and hinder synthesis into a scheme of zonation on a world-wide scale. They also emphasised the need for uniformity in nomenclature, and pointed out that this cannot be obtained by naming zones after locally predominant genera.

The Stephenson therefore put forward a broad scheme of zonation (1949), and are proceeding to examine its world-wide applicability in a series of papers (1950, 1952).

Their scheme is as follows:—

1. *A Supralittoral Fringe*.—At least the lower parts of this are washed or submerged in rough weather or on high spring tides. This zone may be populated by Gastropods such as *Littorina* and *Tectarius*, and by Isopods such as *Ligia*.

2. *A Midlittoral Zone*.—This is covered and uncovered by the tide daily, and may be divided into two zones with barnacles such as *Chthamalus* and *Tetraclita* dominating the upper part.

3. *An Infralittoral Fringe*.—This may be regarded as the upper boundary of a sublittoral zone which is never exposed to the air, and part of this fringe is only exposed on low spring tides.

The Stephenson showed that such a scheme of zonation is related to the principal tidal levels, but is not necessarily coincident with them. The vertical range of a zone, and its vertical position in relation to tidal levels, may be affected by various factors such as the degree of exposure to surf, the amount of shade, etc. Thus the range and level of a certain zone may change considerably, even over a relatively short geographical distance. For these reasons, perhaps, the Stephenson (1950, 1952) did not make exact determinations of the chief tidal levels in their work.

ZONATION OF MARINE FAUNA AND FLORA

Nevertheless, it appears to the writers of the present paper that there are distinct advantages in measuring the vertical ranges of each species with as much accuracy as possible, and in relating the local pattern of zonation to the principal tidal levels. This should remove all doubt from the mind of the reader as to the meanings assigned to any technical terms used, and gives the maximum aid in drawing comparisons with the records of other workers. It is recognized, of course, that the scheme of zonation should not be forced to fit in with the chief tidal levels recorded. It is then a simple matter to disregard the tidal levels, and to simplify the zonation scheme in relating it to a world-wide scheme such as that proposed by the Stephenson.

The writers wish to express their gratitude to the Master Attendant, Singapore, for his kind permission to work at the Raffles Light for a week in July 1952 and another week in October 1952, when the work recorded in this paper was carried out. The authors also wish to record their thanks to Mr. T. W. Burdon, Deputy Director of Fisheries, Singapore, who kindly organised the transport of the party to and from the Raffles Light on each of the above occasions.

Thanks are also due to Mr. M. W. F. Tweedie, Director of the Raffles Museum and Library, for his invaluable help in identifying the Mollusca, and to Dr. E. B. Britton, Department of Entomology, British Museum (Natural History) for his kindness in identifying specimens of *Laius flexicornis*, a beetle found in some abundance on the dry rocks at the top of the beach.

The authors also wish to express their gratitude to Mr. R. Tucker Abbott, of the Smithsonian Institution, Washington 25, D.C., who kindly identified the three species of *Trochus*, and to Dr. Lipke B. Holthuis, temporarily stationed at the Smithsonian Institution, who identified the specimens of *Ligia vitiensis*.

This paper was prepared by the senior author.

Methods

1. Measurement of vertical intervals

Four rulers, each 3 feet long, were secured end to end on a long metal rod. This was then fixed vertically in the water at the end of the Raffles Light Pier, so that the top of the uppermost ruler was in the region of H.W.E.S.T. The rulers were sited so that a reading of the water level could be taken at all stages of tide without inconvenience.

When the water was very calm, it was an easy matter to determine the mean position of the water level, to the nearest inch. When there was a slight swell, this was not so easy, since the range of movement of the water amounted to 10, or 20 inches. It was found, however, that the

readings so taken on a calm day formed a very smooth graph, and it is considered that the error in determining the tidal level at any given time would not amount to more than ± 2 inches. The work was carried out on 27th July and 21st October, 1952, days when the sea was sufficiently calm to achieve this degree of accuracy.

Readings were taken at frequent intervals towards high, and low tide, and at half hour intervals at other times. When all the readings had been taken, a graph was prepared (Figure 1.).

2. Study of the intertidal fauna and flora

On the days that tidal records were being taken as noted above, and starting at high tide, collections were made of species occurring at water level, at regular intervals (usually every half hour) as the tide fell. The collection took approximately the first fifteen minutes of each half hour, and during the remainder of the half hour, a subjective estimate was recorded of the abundance of each species collected.

Collections were made only from rock surfaces, and from very large fixed boulders. The upper and lower levels for each 15 minute sample were obtained from the graphs prepared from the tidal readings.

Evans (1947) showed that satisfactory zonation results were obtained by collecting at the water's edge and calculating the vertical interval above chart datum by reference to tables. A similar technique was adopted here, save that in the warm and calm tropical water it was possible to wade up to the waist in water around the rocks, and collect exactly at the waters edge. In calm weather the estimation of vertical height must have been even more accurate than that by Evans, for the sheltered waters round Singapore can be very calm, and the vertical intervals were measured by ruler only a few yards away from the collecting area.

The Mollusca collected were identified by comparison with named collections at the Raffles Museum, with the aid of Mr. Tweedie. One species, a beetle which was abundant on the upper half of the beach, was identified by Dr. Britton, at the British Museum. The algae were identified by Mr. Enoch.

3. Standardisation of the vertical levels

It would be desirable, if possible, to relate the vertical measurements to some arbitrary standard, so that direct comparisons could be made with records from other shores. The most suitable basis to adopt would be chart datum. Difficulties arise, however, which will be described below and these make it impossible to suggest more than a tentative relationship between the present measured levels and chart datum.

ZONATION OF MARINE FAUNA AND FLORA

Records were made of as many levels of high tide and of low tide as possible during the two visits to the Raffles Light. From these records were obtained observed values for the range of the tide, and these were compared with the ranges predicted in the Tide Tables for 1953.

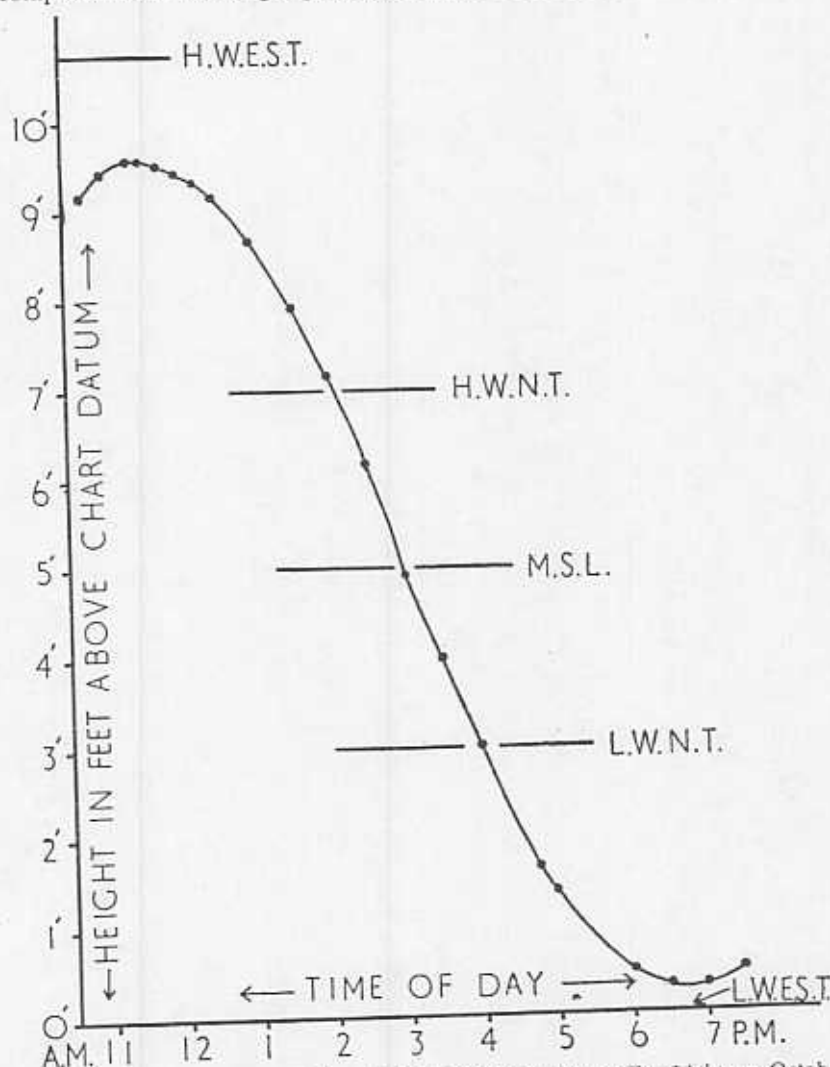


Fig. 1. Graphical representation of tidal movements at Raffles Light on October 21, 1952. H.W.E.S.T. High water of extreme spring tides; H.W.N.T. High water of neap tides; M.S.L. Mean sea level; L.W.N.T. Low water of neap tides; L.W.E.S.T. Low water of extreme spring tides. Zero on the vertical scale represents estimated chart datum.

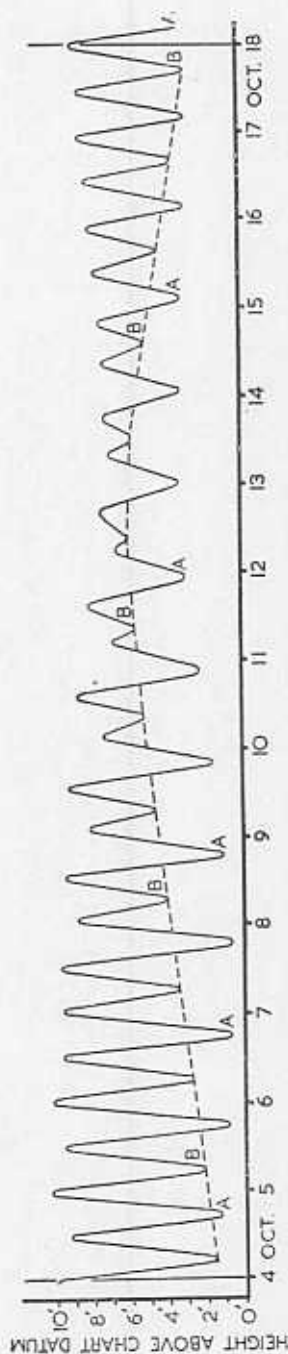


Fig. 2. Graphical representation of tidal movements predicted for Singapore Inner Harbour over a period of 14 days, October 4-18, 1952. Zero on the vertical scale is Chart Datum. Low water marks for the "b" series of tides have been joined by a broken line to indicate more clearly the systematic changes that occur in each tidal cycle. In the next tidal cycle the "a" and "b" tides change over. Heights are in feet.

ZONATION OF MARINE FAUNA AND FLORA

As shown in Figure 2, there is an "a" and a "b" tide each day, and during the period of spring tides one of these tides falls much lower than the other, and has a greater range. Within the admittedly small number of observations of tidal range, it was noted that in the case of the "a" tides, with a great range, the range observed at Raffles Light approximated closely to that predicted for Singapore Inner Harbour, but generally exceeded the expected figure by about 6 inches. On the other hand the "b" tides, with a relatively small range, differed widely from the values predicted for Singapore Inner Harbour, exceeding the predicted figure by as much as 2 feet (see Table I).

TABLE I

Discrepancies between tidal ranges observed at Raffles Light and predicted for Singapore Inner Harbour. Note that the discrepancies are smallest in the case of the "a" tides. The heights recorded for Raffles Light correspond with the vertical scale in Figure 1 and are recorded in feet and decimals of feet.

Date	Raffles Light Observations			Singapore Inner Harbour Predictions			Difference in range
	H.W.	L.W.	Range	H.W.	L.W.	Range	
27th July, 1952 ..	8.3	1.1	7.2	8.8	3.6	5.2	Plus 2.0
21st October, 1952 ..	—	2.0	7.6	—	3.2	6.2	.. 1.4
	9.6	0.3	9.3	9.4	0.7	8.7	.. 0.6 ("a")
22nd October, 1952 ..	—	2.2	7.4	—	3.6	5.9	.. 1.5
	9.6	—	—	9.5	—	—	
23rd October, 1952 ..	—	3.2	7.1	—	4.0	5.5	.. 1.6
	7.1	1.1	9.2	9.5	0.7	8.8	.. 0.4 ("a")
24th October, 1952 ..	—	3.2	6.6	—	4.5	4.8	.. 1.8
	9.8	—	—	9.3	—	—	

Singapore Inner Harbour is protected by the break-water, and by the presence of neighbouring islands, and it is possible that, due to these protecting influences, the tidal wave is damped down somewhat in the Harbour as compared with Raffles Light. This could account for the tidal range being greater by 6 inches at Raffles Light.

The number of observations is far too small to justify a general statement that the greater tides at Raffles Light correspond fairly closely with those at Singapore Inner Harbour, whereas the lesser tides at Raffles Light normally have a range that is greater by 2 feet. Nevertheless, a discrepancy of nearly 2 feet on a calm day, recorded on more than one occasion removes the matter from the realms of observational error.

It was of great interest to learn from Capt. W. Groom, of the Anglo-Saxon Petroleum Co. (Eastern), Ltd., in a personal communication, that a tide pole had been set up on the north side of Pulau Bukom,

and that a series of readings had been taken over the period 30th June, 1952 to 17th August, 1952. On one of these days, 27th August, 1952, series of tidal readings had been taken both at Pulau Bukom and at Raffles Light. It was extraordinary to learn that the tidal range recorded at Pulau Bukom on that day agreed closely with that predicted for Singapore Inner Harbour, when a difference of plus 2.0 feet was recorded at Raffles Light only a few miles away.

The only reason that the writers can offer for the difference in tidal range between Pulau Bukom and Raffles Light, as noted above, is that Raffles Light experiences the full range of tide in the open channel, but that in the protection of the islands, the tidal range is reduced.

It remains to explain why the greater tides should be damped down only slightly in the protection of the breakwater and islands, while the lesser tides should be so markedly reduced. Before this should even be considered, it would be desirable to make extensive observations on the tidal range at Raffles Light and at as many other local stations as possible, so as to confirm or disprove the indications of the above records. Until this is done, it will not be possible to determine chart datum at Raffles Light.

As a temporary expedient, it is suggested that the "a" tides at the time of spring tides have a greater range at the Raffles Light than at Singapore Inner Harbour, and that the increase in range is symmetrically disposed about M.S.L. On 21st October, 1952 the tidal range at Raffles Light was 9.25 feet whereas that predicted for Singapore Inner Harbour was 8.7 feet. Low tide at Raffles Light on that day would thus have been 0.7 feet—0.27 feet — about 0.4 feet above chart datum. Graph I was therefore drawn with the estimated position of chart datum at zero.

In the present account, all measurements are in feet and inches above "estimated chart datum". On this basis, the upper of two marks at the end of the pier at the Raffles Light is approximately 10 feet 0 inches above estimated chart datum. High water mark of extreme spring tides comes about 9 inches above this mark.

The Tidal Regime

The month of October 1952 was taken as an example, and Figure 2 was prepared of the times and heights of high water, low water, and intervening levels throughout fourteen days (as predicted in the Tide Tables for 1952 for Singapore Inner Harbour). The resulting graph differs so markedly from what would be found for an open beach in British waters that some comment on the unusual conditions is necessary.

ZONATION OF MARINE FAUNA AND FLORA

During Spring Tides only one really low tide occurs per day. From April until September this low spring tide occurs early in the morning, whilst from October until March the low spring tides occur in the evening. The lowest levels of the beach are therefore never exposed to the greatest heat of the tropical sun.

The two low tides for each day change in level independently, and their graphs intersect a few days before each set of spring tides. After this intersection, one low tide (which had been a very low tide a week before) increases gradually in level from day to day until it even rises above mean sea level (tide "b"); the other low tide falls slightly in level for a few days, to become the low spring tide of that cycle (tide "a").

The same may be said of the high tides, except that the difference in height between the two high tides of any one day is of a smaller order. Consequently, a few days before a period of spring tides there is a short interval when the two tides per day are almost of the same amplitude. At the peak of the spring tides the two high tides coincide approximately in level, whilst the lesser low tide is over three feet higher than the greater.

Finally at Neap Tides, the lesser tide has become a mere 7 inch secondary peak on the side of the major tide, and its low tide is a foot above mean sea level.

It follows that the High Water of Neap Tides (H.W.N.T.) can be defined as the lowest level to which the higher of two adjacent high tides can fall. Similarly, Low Water of Neap Tides (L.W.N.T.) should be defined as the highest level reached by the lower of the two adjacent low tides.

Figure 2 refers to the tidal conditions in Singapore Inner Harbour. The discrepancies between tidal ranges observed at Raffles Light and predicted for Singapore Inner Harbour suggest that the difference between the levels of low water for "a" and "b" tides at Raffles Light is not so great as shown in Figure 2.

Colman (1932), at Plymouth, prepared graphs similar to Figure 2 for four representative fortnights in the year, and obtained from these graphs an estimate of the number of hours of exposure in the year at a series of levels above chart datum. He was then able to prepare a graph depicting the percentage exposure at each level on the beach.

In the region of Singapore, however, the seasonal differences in level of low water mark of spring tides are very slight. It was therefore considered sufficiently accurate to determine the percentage exposure by consideration of a single representative period of one fortnight. This was done by measuring, on a large scale graph, the number of hours of

exposure during one fortnight at each of eleven levels on the beach, at one foot intervals, and expressing the results as a percentage. The results given in Figure 3 (continuous line) refer to Singapore Inner Harbour.

On the same graph is included for comparison the estimated percentage exposure on a beach on Anglesey, North Wales (broken line) (Glynne-Williams & Hobart, 1952). The vertical scales have been adjusted so that the principal tidal levels (H.W.E.S.T., H.W.N.T., M.S.L., L.W.N.T., L.W.E.S.T.) for the two beaches are at corresponding levels on the graph. It can be seen at a glance that, due to the peculiar tidal conditions in the vicinity of Singapore, at all levels on the beach, the Singapore rocks are uncovered for a shorter period than are rocks at the same relative level on the coast of Anglesey.

There is at least 5 per cent longer immersion at Singapore Inner Harbour at all levels except in the near vicinity of H.W.E.S.T., and L.W.E.S.T., but it will be noticed that the greatest difference is between L.W.N.T. and a foot above M.S.L., where there is from 10 per cent to 20 per cent extra immersion at Singapore.

Extensive tidal observations at Raffles Light may show that, with regard to percentage exposure of the rocks, the shore at Raffles Light is intermediate in condition between the estimates for Singapore Inner Harbour and Anglesey as shown in Figure 3.

The Algae

With regard to the algae, the intertidal zone can be sub-divided into two major zones. Above L.W.N.T., numerous species are present, but are not sufficiently abundant, or sufficiently large, to combine to form an algal canopy. This part of the beach is exposed daily to sun and wind, and the absence of an algal canopy must be of great importance with regard to the distribution of the fauna. Below L.W.N.T., the conditions are otherwise. Many of the same species as occur above L.W.N.T. are present below this level, but here they are abundant, and collectively may form a relatively luxuriant canopy, which will provide both food and protection to a host of animal species.

The rich growth of algae here is doubtless due to the greater infrequency, and shorter duration of exposure, and also to the fact that they are not exposed to the heat of the mid-day sun.

The distribution of the algae was recorded as follows.

Group I. From H.W.E.S.T. to H.W.N.T.

Only microphytic species of algae (which have not been identified), on the rock surfaces, and in rock crevices.

ZONATION OF MARINE FAUNA AND FLORA

Group II. From H.W.N.T. to L.W.N.T.

Green *Ulva reticulata* Forskal.

Also, occasional and small specimens of all the species listed in Group III.

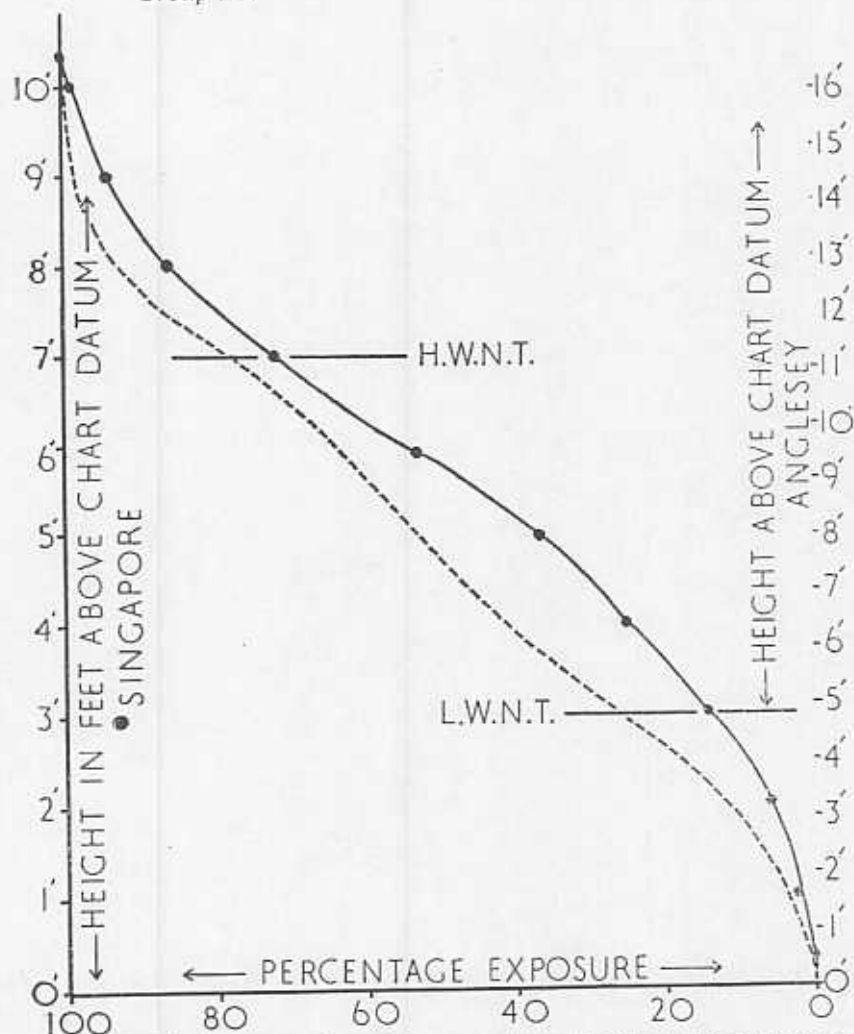


Fig. 3. Graphical representation of the percentage exposure of the rocks to the air at different levels on the beach, Singapore Inner Harbour (continuous line); Anglesey (broken line). The two curves are drawn to different vertical scales so that their principal tidal levels coincide. H.W.N.T. High water of neap tides; L.W.N.T. Low water of neap tides.

Group III. From L.W.N.T. to L.W.E.S.T.

- Brown *Turbinaria ornata* J. Agardh.
Sargassum siliquosum J. Ag.
Colpomenia sinuosa Roth., Derbes et Solier
Hydroclathrus cancellatus Bory.
Padina Commersonii Bory.
- Red *Acanthophora spicifera* Vahl., Borg.
Sphaerococcus sp. C.A. Ag.
Lithothamnion erubescens Foslie
Eucheuma edule Kütz
Halymenia Durvillaei Bory.
- Green *Dictyosphaeria favulosa* Agardh.
Bryopsis plumosa J. Agardh.
Caulerpa taxifolia Vahl.
Caulerpa racemosa Forskal.
Avrainvillea erecta Murray & Boodle
Halimeda Opuntia Lamouroux
Halimeda Tuna Lamouroux.

Group IV. Below L.W.E.S.T.

- Brown *Turbinaria ornata* J. Agardh. (large plants)
Sargassum siliquosum J. Ag. (large plants)
- Red *Eucheuma edule* Kütz
Eucheuma striatum Schmitz
Eucheuma muricatum Gmelin
Halimena Durvillaei Bory.
- Green *Caulerpa Freycinetii* Ag.
Caulerpa racemosa Forskal
Caulerpa peltata var. *macrodisca* Decaisne

The Fauna

Before proceeding to a consideration of the zonation of various species, reference must be made to four species, the behaviour of which necessitates separate treatment.

1. *Laius flexicornis* Fabr. This beetle (Malachiidae) was found in abundance on dry rocks above H.W.N.T. It presumably sheltered in crevices during high tide, and when uncovered by the tide it was found crawling widely over the rocks.

ZONATION OF MARINE FAUNA AND FLORA

2. *Ligia vitiensis* Dana. This Isopod is crowded together in crevices in the upper part of the beach while the tide is high, and was consequently not seen in the collections taken at the water's edge. As the tide recedes, however, it spreads widely over the rocks, following the retreating water.

3. *Oncidium* (?) sp. These slugs creep into rock crevices while the tide is high, and only emerge after the tide has fallen. Only infrequent specimens were seen at the water's edge, yet a glance over the dry rocks above showed them crawling in abundance over the rocks above M.S.L. approximately.

4. *Metopograpsus oceanicus* (Jacq. & Lucas). These crabs occupy an ecological niche which is complementary to the Isopods mentioned above. They lurk at, or slightly above the water level, always keeping wet, and recede with the ebbing tide.

Next, mention must be made of the tactic movements of *Littorina undulata* and *Tectarius malaccensis*. These two species occur above M.S.L., and are chiefly to be found in clusters on the wet rocks immediately above the water's edge. While the tide is falling, these two species crawl downwards in pursuit of the water, and if the rocks are vertical and smooth they are able to keep up with the water's edge, even in the vicinity of M.S.L., when the tide is falling at its maximum speed. Specimens of *L. undulata* were studied on the smooth vertical pillars of the pier, and were seen to crawl 6 feet downwards during one tide, and appeared to be stopped only by a zone of large and rough barnacles. Near M.S.L. they crawled at the rate of 14 inches in 30 minutes.

On the open rocky shore, however, the rocks are not vertical, and they are beset with irregularities and here these two species are not able to crawl downwards sufficiently quickly to keep level with the ebbing tide. After a time, they are left behind on the rapidly drying rocks, and they then secure themselves, perhaps in some small crevice. When the tide rises again, they will be activated by the splashes of water, and will ascend with the rising tide. Thus, although the level of high tide varies abruptly from tide to tide, as explained in the previous section, and as illustrated in Figure 2, these diurnal migrations may enable *Littorina undulata* and *Tectarius malaccensis* to maintain their positions on the beach with relation to the high tides.

With regard to the remainder of the Gastropoda, doubtless the majority undergo diurnal movements of a similar nature in relation to the movements of the tide, but since these movements are principally below the surface of the water, we cannot estimate their extent. We can, however, record the zones on the beach within which they are to be found when exposed by the ebbing tide.

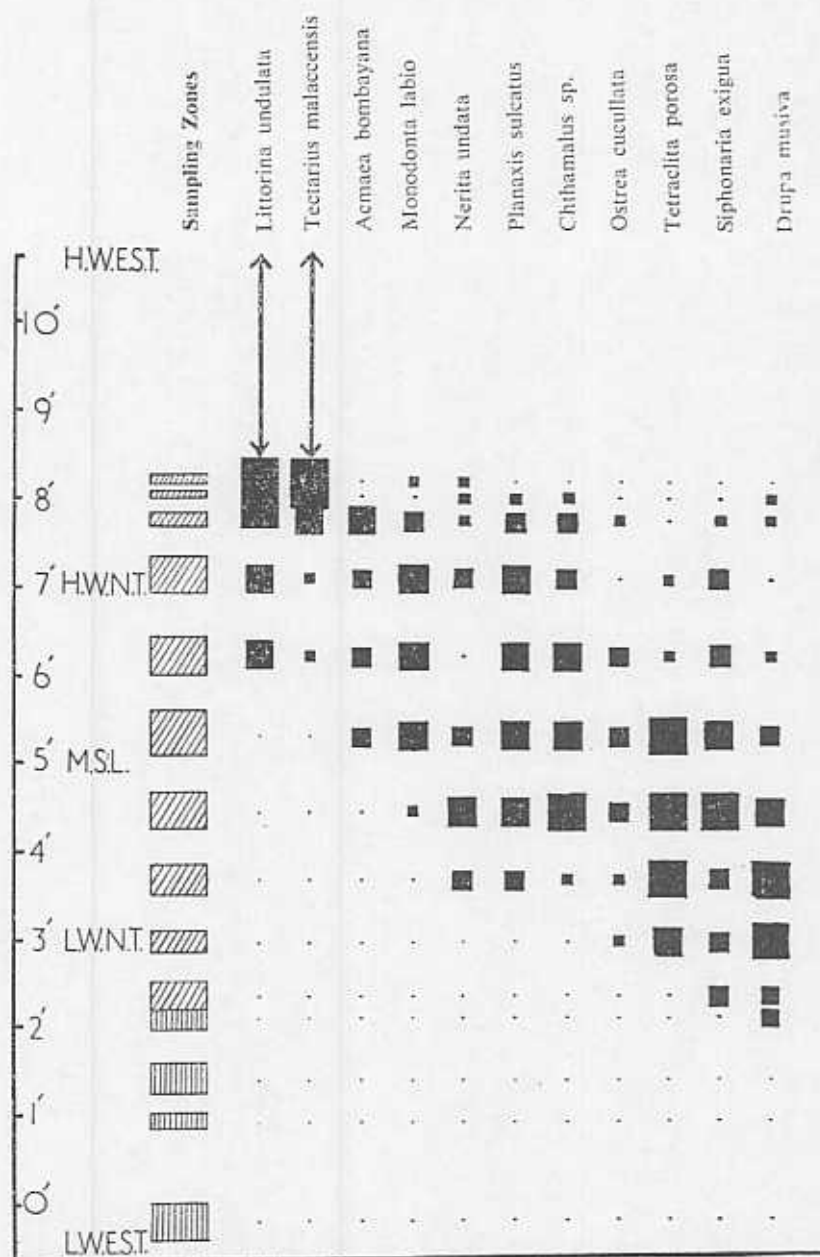
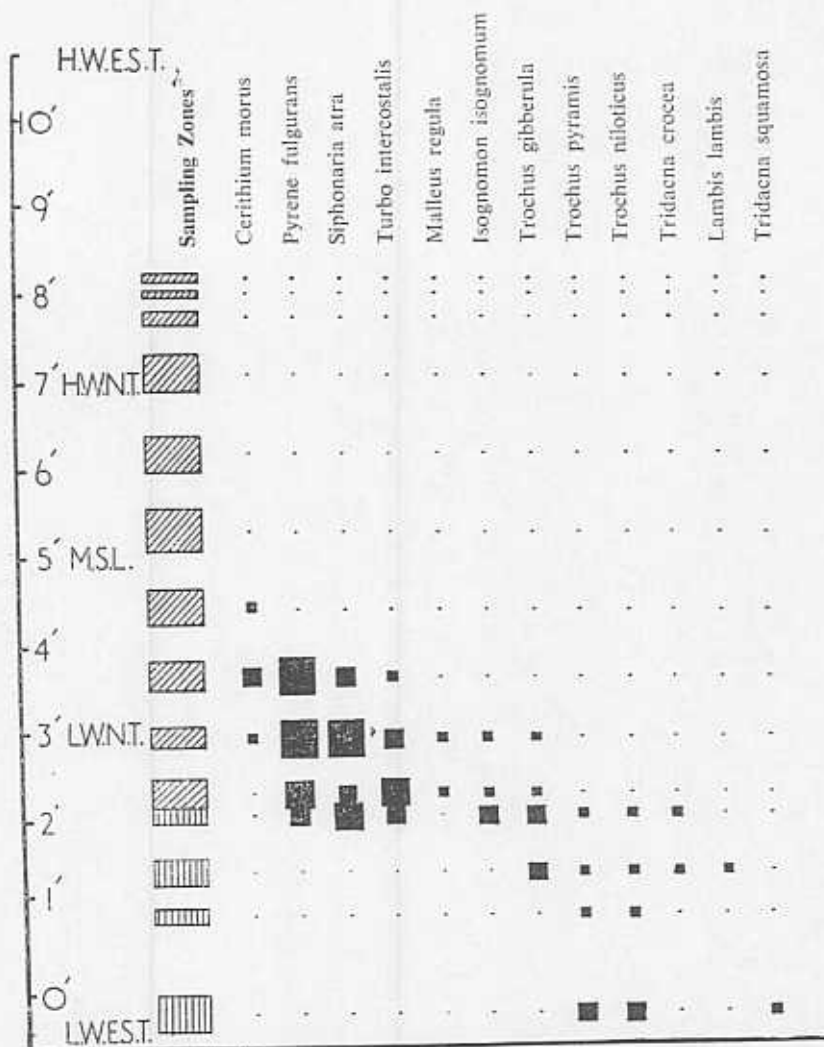


Fig. 4. Diagrammatic representation of the vertical distribution of 23 species of animals at Raffles Light. Zero on the vertical scale represents estimated chart datum. The hatched rectangles adjacent to the vertical

ZONATION OF MARINE FAUNA AND FLORA



scale represent the vertical position, and thickness of the zones in which collections were made. The relative abundance of each species at each level on the beach (estimated subjectively) is indicated by the size of the black squares. A small dot indicates absence of a species at a particular level. The black squares are of four sizes, increasing in area geometrically. Smallest square (1 unit in area) indicates "rare". Second square (4 units in area) indicates "occasional". Third square (9 units in area) indicates "common". Largest square (16 units in area) indicates "abundant". The terms rare, occasional, common and abundant are used independently for each species.

We have already defined High Water of Neap Tides, and Low Water of Neap Tides, as applicable to shores in the vicinity of Singapore. It is interesting to find that these levels have some significance with regard to the zonation of intertidal animals and plants. The beach can be roughly divided into three horizons: Rocks above H.W.N.T., which are left dry for not less than one whole day, and up to fourteen days per fortnight; rocks between one foot above H.W.N.T.¹ and one foot below L.W.N.T., which are mostly exposed, and submerged at least once every day; rocks below L.W.N.T., which are wholly submerged on at least one day, and up to fourteen days per fortnight. This region is only exposed after about 3.30 p.m. and so is not subjected to the greatest heat of the sun.

As determined above, these three zones have the following vertical measurements respectively:—33 inches, 72 inches, and 28 inches. Division of the beach into these three zones is ecologically justified, for the littoral fauna can be subdivided naturally into the following four groups according to the vertical distribution of each species (see Figure 4).

Group I. From H.W.E.S.T. to M.S.L.

Tectarius malaccensis (Phil.), *Littorina undulata* Gray, and *Acmaea bombayana* Smith. Although these three Gastropod species extend considerably below H.W.N.T., they are the chief species which can live on the hot and dry rocks above H.W.N.T. *Acmaea bombayana* is relatively stable in its position, and was found in greater abundance above H.W.N.T. than below this level. The remaining two species are very active animals, and follow the tide as it rises and falls, as noted above. Although they extend below H.W.N.T., they do this on an ebbing tide, and can best be regarded as typical of the uppermost zone of the beach.

Group II. From H.W.N.T. to L.W.N.T.

To be included here, are the Gastropods *Drupa musiva* Kien., *Monodonta labio* (L.), *Planaxis sulcatus* (Born.), *Nerita undata* L., and *Siphonaria exigua* Sowerby, the Lamellibranch *Ostrea cucullata* Born., and the Cirripedes *Tetraclita porosa* (Gmel.), and a species of *Chthamalus*.

Of these, the records show that the Gastropods *M. labio*, *P. sulcatus* and *N. undata* do occasionally crawl above H.W.N.T. as the tide rises, but are crawling downwards again as the tide recedes, and may occasionally be exposed at levels above H.W.N.T. Similarly specimens

¹. To allow for splashes.

ZONATION OF MARINE FAUNA AND FLORA

of *Chthamalus* and *O. cucullata* occur occasionally above H.W.N.T., but these are usually found in shallow pools, or small crevices that retain a little water. *D. musiva* may be found a little below L.W.N.T.

Thais echinata (Blainville) is characteristic of this zone, and may be found in association with the barnacle *Tetraclita*, on which it probably feeds. It was encountered too infrequently to justify plotting its vertical range.

Group III. Species occurring chiefly at L.W.N.T., and extending a short distance above and below.

This group includes four species of Gastropoda, namely *Cerithium morus* Lam., *Pyrene fulgurans* (Lam.), *Turbo intercostalis* Mencke, and *Siphonaria atra* Quoy & Gaimard. This group may be regarded as an advance guard from the typically sublittoral species, into the more rigorous littoral zone (except the Pulmonate, *Siphonaria*).

Group IV. Species which occur below L.W.N.T.

The total number of species so far recorded as occurring above L.W.N.T. is only fifteen, plus the four species considered separately above. Below L.W.N.T. the biological conditions are far less rigorous. This zone is only exposed for short intervals of time to the heat of the sun and to dessication. These periods of exposure are confined to the early morning and to the late afternoon, and not to the full heat of the day. Finally, it is only in this zone that we find an adequate algal canopy, comprising three species of *Sargassum* and several other species of seaweed, which provide both protection against heat and dessication, and also a source of food for herbivorous animals. The fauna and flora of this zone are best regarded as representing the upper margin of the sublittoral zone. Although there are many species characteristic of this zone which cannot extend downwards below L.W.E.S.T., there is a great number of species which live equally well above and below L.W.E.S.T.

It is in this zone, below L.W.N.T., that the greatest diversity of life is to be found, both in tropical and in temperate waters. No attempt will be made here to deal with the vast number of species that may be encountered in this zone; attention will be given only to a small number of characteristic, and easily recognised forms.

The facies is given chiefly by seaweeds, especially the species of *Sargassum*, by alcyonarians (soft corals), and to a lesser extent by corals. The most characteristic Gastropods are *Lambis* (*Pterocera*) *lambis* (L.), *Thais echinulata* (Lam.), and *Trochus gibberula* A. Adams. The Lamellibranchia include *Tridacna crocea* Lamarck, which burrows into coral boulders, and also *Hippopus hippopus* (L.) and

Tridacna squamosa Lamarck, related forms which do not burrow, however, but lie unattached, anchored solely by their weight. *Malleus regulis* Forskal, and *Isognomon isognomum* (L.) also occur occasionally, attached by byssus threads, and usually wedged securely in a crevice.

Mention should be made of the zonation of the three species of *Trochus* which have been found. *T. gibberula* was listed above as characteristic of the zone between L.W.N.T. and L.W.E.S.T. *Trochus (Tectarius) pyramis* Born tends to replace *T. gibberula* in the vicinity of L.W.E.S.T., and, below L.W.E.S.T., is itself replaced by a larger species in the same genus, *T. niloticus* L.

Discussion

The scheme of zonation which has been derived from studying the rocky shore of the Raffles Light agrees well with the scheme put forward by the Stephenson (1949, 1950, 1952). The uppermost zone, approximately above high water mark of neap tides may be regarded as the Supralittoral Fringe, and contains representatives of the genera predicted by the Stephenson, e.g. *Littorina*, *Tectarius* and *Ligia*.

The middle zone, between one foot above high water mark of neap tides and one foot below low water mark of neap tides can be equated with the Midlittoral Zone of the Stephenson and is likewise divisible into an upper zone populated by species of barnacles in the genera *Chthamalus* (above) and *Tetraclita* (a little lower). Other genera indicated by the Stephenson are also present, e.g. the limpet *Siphonaria*, the dog whelk *Thais*, the slug *Oncidium* and the bivalves *Ostrea* and *Isognomon*.

The lowermost zone, passing downwards from about one foot below low water mark of neap tides, can be regarded as the Infralittoral zone. Here the number of species is very large, and has not been studied in any detail in the present paper. Again there are numerous points of comparison with the work of the Stephenson, e.g. the algae *Halimeda*, *Padina*, *Caulerpa*, *Sargassum*, etc., and various genera of corals (which have not been treated here) are present, as anticipated.

The number of species which have been listed from the rocks above low water mark of neap tides is rather small. This is partly due to a number of factors:—collecting was confined to "macroscopic" species on exposed rock surfaces; there were no overhangs to investigate, and no attempt was made to open rock crevices. Apart from these qualifications, the small number of species recorded is doubtless a consequence of the great heat and dessication experienced above low water mark of neap tides, and to the absence in this area of an algal canopy.

ZONATION OF MARINE FAUNA AND FLORA

Comparison with shores on open coasts in British waters (Colman, 1932; Glynn-Williams & Hobart, 1952) indicates that shores in the immediate vicinity of Singapore have from 5 per cent to 20 per cent more protection from heating and dessication, as they are covered longer by the sea. But for this extra protection, doubtless fewer species would have been recorded above low water mark of neap tides, and perhaps the range of many of these species might have been lower on the beach. It is possible that this peculiar tidal regime, and the special protection afforded by it to the intertidal fauna and flora would not be found on open coasts in the north of Malaya.

It is hoped that further studies of the zonation of the intertidal fauna and flora around the coasts of Malaya will amplify, and perhaps correct the present account. As mentioned by Evans (1947), at any one locality a species may not occupy the whole of its potential range. The settlement of other and competing organisms may limit the vertical range of a species on any one beach, or in any one season.

References

- BARTON, E. S., 1901. The Genus *Halimeda*. *Siboga Expedit.* LX.
- COLMAN, J., 1932. The nature of the intertidal zonation of plants and animals. *J. Mar. Biol. Ass. U.K.* N.S. 18, 435.
- EVANS, R. G., 1947. The intertidal ecology of selected localities in the Plymouth neighbourhood. *J. Mar. Biol. Ass. U.K.* N.S. 27, 173.
- FRITSCH, F. E., 1948. *Structure and Reproduction of the Algae*. Vols. 1 & 2. Cambridge.
- GEPP, A. & E. S., 1911. The Codiaceae of the Siboga Expedition. *Siboga Expedit.* LXII.
- GLYNNE-WILLIAMS, J. & HOBART, J., 1952. Studies on the crevice fauna of a selected shore in Anglesey. *Proc. Zool. Soc. Lond.* 122, 797.
- MANTON, S. M., 1935. Ecological Surveys of Coral Reefs. *Brit. Mus. Nat. Hist. Great Barrier Reef Expedition.* 3, 273-312.
- STEPHENSON, T. A. & A., 1949. The universal features of zonation between tide-marks on rocky coasts. *J. Ecol.* 37, 289.
- , 1950. Life between tide-marks in North America. 1. The Florida Keys. *J. Ecol.* 38, 354.
- , 1952. Life between tide-marks in North America. 11. Northern Florida and the Carolinas. *J. Ecol.* 40, 1.
- TIDE TABLES FOR MALAYA, NORTH BORNEO AND SARAWAK, 1952.
- WEBER VAN BOSSE, A. & FOSLIE, M., 1904. The Corallinaceae of the Siboga Expedition. *Siboga Expedit.* LXI.
- WEBER, A., 1913-1928. Liste des algues. *Siboga Expedit.* LIX.